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PERSPECTIVE

Discontinuous gas exchange: new perspectives on evolutionary origins and ecological implications

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Summary

1. When at rest, many insects and some other arthropods exchange gasses discontinuously. Whether or not discontinuous gas exchange (DGE) is adaptive has long been controversial. Several competing evolutionary hypotheses exist, none of which enjoy unequivocal support. This Gordian knot seems now to have been cut.

2. Discontinuous gas exchange appears to arise as a consequence of energy-saving, metabolic downregulation. Moreover, many ecological circumstances, such as quiescence during daily inactivity and during seasonal resource shortages, are likely to have favoured such downregulation.

3. Once the brain relinquishes control of gas exchange to the segmental ganglia, an interaction between peripheral CO_2 sensing and central O_2 sensing sets in, leading to the discontinuous pattern.

4. The evolution of DGE may thus be readily explained, with the primary evolutionary hypothesis incorporating a non-adaptive mechanistic component and an adaptive energy savings one.

5. Paradoxically, though, DGE results in a comparatively high water loss for a given metabolic rate in insects compared with other organisms. Thus, the pattern itself may not have evolved to limit water loss under xeric conditions. Rather, variation in the components of the DGE cycle, which has formed the foundation for much debate concerning the ecological and evolutionary advantages of this gas exchange pattern, may have evolved to do so, accounting for associations between these components and environmental conditions.

6. The relatively high respiratory water loss of insects may spell ecological trouble given increasing metabolic rates of ectotherms associated with rising global temperatures and global change–type drought in many regions.

Key-words: arthropods, gas exchange, global change, hypoxia, metabolic rate, water loss

Discontinuous gas exchange in arthropods

Discontinuous gas exchange (DGE) has long been considered one of the most enigmatic gas exchange patterns found in animals. Although periodic breathing is typical of many vertebrates (Milsom 1991; Fong, Zimmer & Milsom 2009), several tracheated arthropod taxa show, when at rest, a unique, three-phase, cyclic pattern of gas exchange. Originally, the pattern was characterized with reference to the behaviour of the spiracles, the external openings of the tracheae – the air tubes that convey respiratory gasses to and from the tissues in insects and other arthropods. Subsequently, DGE has most commonly been identified using either gas (usually $\dot{V}CO_2$) traces from high-resolution, flow-through respirometry or simultaneous measurement of gasses (see Lighton 2008 for a general discussion of gas exchange in animals) and pressure change within the tracheal system (illustrations of a pressure change system are provided by Terblanche *et al.* 2008). A closed (C) phase of no gas exchange through the spiracles is followed by a flutter (F) phase where gas exchange is minimal and the spiracles rapidly flutter open and closed, and then by an open (O) phase where most exchange takes place (Lighton 1996; Chown *et al.* 2006; Quinlan & Gibbs 2006) (Fig. 1). The pattern then repeats, accounting for the term discontinuous gas exchange cycle (DGC).

Discontinuous gas exchange was discovered in insects nearly a century ago, but it is not evident in all tracheated

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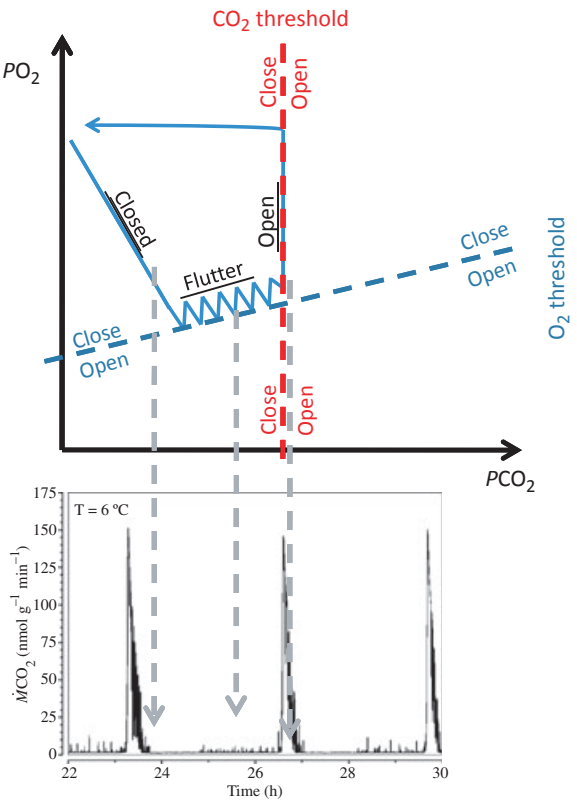


Fig. 1. The phase space model (Förster & Hetz 2010), based on endotracheal O_2 and CO_2 concentrations, is shown in the upper panel and the corresponding areas on a $\dot{M}CO_2$ trace from flow-through respirometry on the lower panel. Discontinuous gas exchange phases are underlined in the upper panel and connected by grey lines to the corresponding areas of the respirometry trace. Spiracles remain closed when the endotracheal PO_2 is above its threshold value (blue dashed line) and the PCO_2 below its threshold (red dashed line). Endotracheal PO_2 then decreases owing to respiration and PCO_2 increases for the same reason, although more slowly because of buffering of CO_2 in the body tissues and fluids. When the PO_2 threshold is reached the flutter phase commences because of a recurring delay in feedback caused by the time it takes O_2 to reach the segmental ganglion, where it is sensed, once the spiracle has opened. As soon as PCO_2 rises above its threshold value the spiracles open. The spiracles then remain open as CO_2 is purged not only from the tracheal system but also from the haemolymph buffering system, hence the prolonged open phase. Note that respirometry trace measurements and endotracheal pressure measurements do not always correspond because the latter can detect the early stages of the F phase when the former cannot because of the incurrent air stream (Chown *et al.* 2006). Redrawn using as a basis figures from Förster & Hetz (2010) and Moerbitz & Hetz (2010).

arthropod groups, nor indeed in all of the insect species that have been examined. Among the insects, of the 18 orders that have had species included in the appropriate experimental trials, DGE has thus far been found only among the cockroaches, locusts, grasshoppers, beetles, moths, bees and ants (Marais *et al.* 2005), although these groups account for much of extant insect diversity. Why these insects and the members of a few other arthropod taxa (Box 1) should show such a strange pattern of gas exchange, what adaptive value DGE may have, if any, how it originated, and why insects generally show such a diversity of breathing patterns are contentious matters that have been the source of a protracted controversy among evolutionary physiologists (Levy & Schneiderman 1958; Kestler 1985; Lighton 1998; Chown *et al.* 2006; Bradley 2007; Socha, Förster & Greenlee 2010).

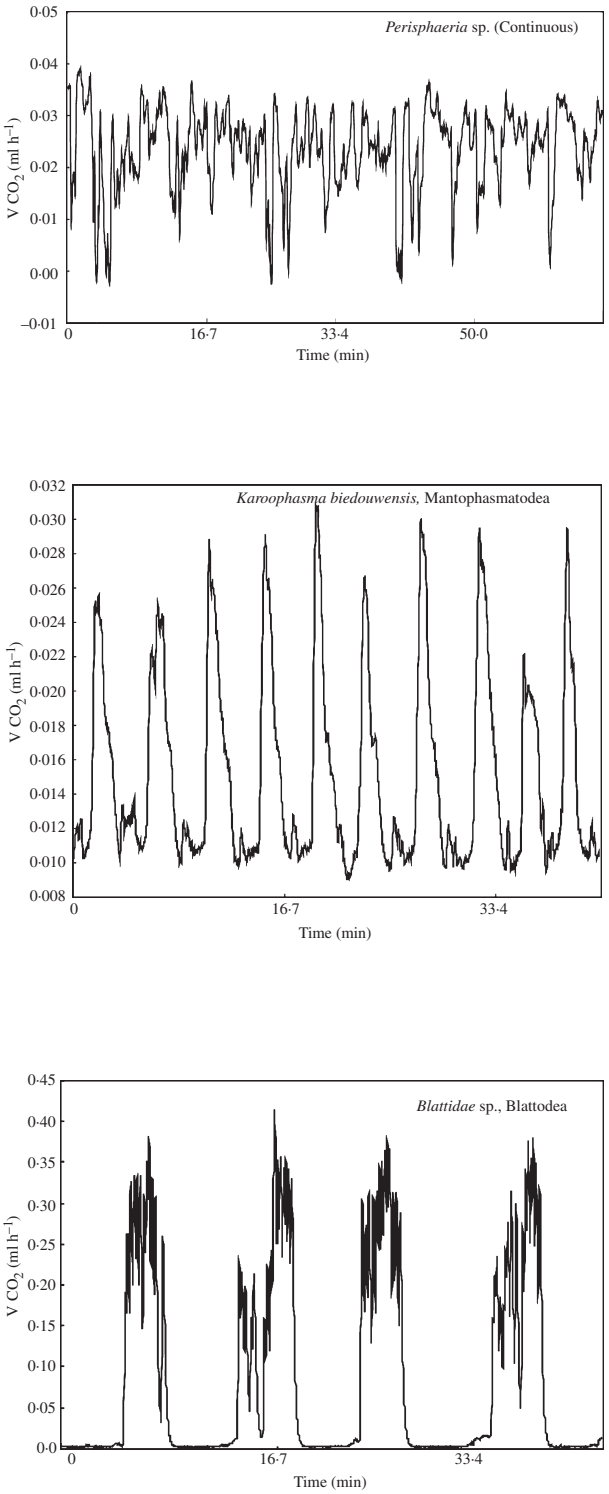
Multiple adaptive hypotheses

Early work settled on the reduction in respiratory water loss as an adaptive explanation for DGE (known now as the hygric hypothesis). Closed spiracles limit water loss via the tracheae, and during at least the early parts of the F phase, a negative endotracheal pressure, causing bulk flow inward, prevents water egress whilst oxygen is entering the system (Buck, Keister & Specht 1953; Levy & Schneiderman 1966). However, after nearly 30 years of the case being considered closed, it was reopened in the 1990s when a variety of evidence suggested that respiratory water loss might not account for the pattern: respiratory water appears to contribute little to total water loss; F phase gas exchange might be predominantly diffusive meaning little pressure differential to prevent outward movement of water vapour; some desert-dwelling species do not show DGE; dehydrated individuals that might be expected to show the pattern often relinquish it; and individuals at high temperatures, where saturation deficits are high, often abandon DGE (Hadley & Quinlan 1993; Lighton & Berrigan 1995; Lighton 1996; Chown 2002). A variety of alternative adaptive hypotheses followed. These include the need for gas exchange in hypoxic and hypercapnic environments either with or without considering water loss (chthonic and chthonic–hygric hypotheses), the exclusion of parasitic species (Harrison *et al.* 2001) (strolling arthropods hypothesis) and the reduction in oxidative damage that would result, during low oxygen demand, from a gas delivery system evolved to meet metabolic demand during strenuous activity such as flying (oxidative damage hypothesis, Hetz & Bradley 2005) (reviewed in Chown *et al.* 2006).

The literature examining these alternatives has burgeoned, with each of the hypotheses variously being found either wanting or robust (Duncan & Byrne 2000; Chown & Davis 2003; Gibbs & Johnson 2004; Hetz & Bradley 2005; Lighton & Ottesen 2005; Lighton & Turner 2008; Terblanche *et al.* 2008; Schimpf, Matthews & White 2009). Moreover, the landscape has further been complicated in two ways. First, a non-adaptive hypothesis was introduced (Chown & Holter 2000), suggesting that under conditions of low metabolic demand, DGE arises as a consequence of interactions between the PO_2 and PCO_2 set points that regulate spiracle opening, at least one of which (PO_2) might involve a central pattern generator found in the segmental ganglia of insects (rather than in the ganglia in the head that constitute the brain) (Bustami & Hustert 2000; Chown & Holter 2000). Second, arguments have been made that DGE is one endpoint of a continuum of gas exchange patterns (Bradley 2007; Contreras & Bradley 2010). Thus, DGE predominates during low metabolic demand when closed spiracles are the norm. As metabolic demand increases, gas exchange becomes cyclic,

Box 1. Discontinuous, cyclic and continuous gas exchange

Many insects and their relatives among the arthropods and related taxa have now been examined for the form of their gas exchange pattern. In those groups without spiracles that can close, or that lack a tracheal system entirely, gas exchange is always continuous. However, gas exchange may also be continuous in taxa with occludable spiracles and with good control of them. Using flow-through respirometry (typically CO_2 is measured using infra-red gas analysis), continuous gas exchange is defined as the absence of any period of zero gas exchange and an equal distribution of data both above and below the average value (typically of $\dot{V}CO_2$ or $\dot{M}CO_2$), or perhaps more data above it (Marais *et al.* 2005) (panel (a) in the figure below). Taxa showing continuous gas exchange at rest include velvet worms (Onychophora) (Clusella-Trullas & Chown 2008), some centipedes (Klok, Mercer & Chown 2002), mites (Lighton & Duncan 1995), harvestmen (Lighton 2002) and several insect groups (Marais *et al.* 2005). Active arthropods all show continuous gas exchange, although those with spiracles may still alter the aperture thereof, so affecting the pattern of gas exchange, to save water (Lehmann & Schützner 2010). Cyclic gas exchange (panel b) is characterized by more regular peaks and troughs of gas exchange. Formally, it has been suggested that if less than 30% of the data lie above the average value (typically of $\dot{V}CO_2$ or $\dot{M}CO_2$) in a gas exchange trace, the pattern is cyclic (Marais *et al.* 2005). When at rest, groups such as the pseudoscorpions and many insects show cyclic gas exchange (Lighton & Joos 2002; Marais *et al.* 2005). Indeed, it has been suggested that cyclic and continuous gas exchange are basal in the insects and DGE more derived, having arisen independently several times in this group and in other arthropods. Discontinuous gas exchange (DGE, panel c) comprises periods when the spiracles are closed and gas exchange does not take place, followed by a flutter phase characterized by small openings of the spiracles, often, though not always detectable by CO_2-based respirometry, and followed a typically short open phase that usually is evidenced as a burst of CO_2 release. The open phase may or may not be accompanied by active ventilation. DGE has now been found in many species of cockroaches, locusts/grasshoppers, beetles, bees, ants and the pupae of moths (Marais *et al.* 2005; White *et al.* 2007), as well as in centipedes, solifuges and ticks. Some authors, such as Bradley (2007) and Contreras & Bradley (2010), are of the view that these gas exchange patterns form a continuum, with DGE occurring at low metabolic demand. That DGE manifests only during rest has long been appreciated (Lighton 1996).



with the spiracles not closing fully. Finally, continuous gas exchange occurs during high metabolic demand when the spiracles are typically open or at least do not close entirely even though their aperture may be regulated (Lehmann & Schützner 2010). According to this view, DGE should not be considered a discrete pattern of gas exchange found in some taxa, but not others, and that deserves to be singled out for particular attention (Bradley 2007).

Recently, increasingly sophisticated experimental and comparative work, adopting a strong inference approach, seems

to be settling on the oxidative damage and hygric hypotheses as the most appropriate adaptive explanations for DGE (White *et al.* 2007; Terblanche *et al.* 2008; Schimpf, Matthews & White 2009). Nonetheless, the field has remained in a state of multiple competing, and seemingly irreconcilable, hypotheses (Lighton 2007), with apparently little prospect for resolution. Moreover, much of the work has drifted away from considering, simultaneously, mechanistic and evolutionary explanations for the origin and maintenance of these cycles.

Resolution?

This Gordian knot now seems to have been cut. Using a technically demanding, experimental perfusion protocol, and a phase space diagram approach, Förster & Hetz (2010) provide empirical support for a new spiracular control model that explains the time course of endotracheal partial pressures during DGE and the alternation between closed, open and flutter phases. Their model is elegant and simple (Fig. 1). The model assumes that both CO_2 and O_2 are involved in regulating spiracle behaviour, that the CO_2 partial pressure threshold for spiracle opening is sensed at the spiracle muscle with little central nervous input and that the O_2 partial pressure threshold is sensed in the segmental ganglia of the central nervous system. These assumptions are all in keeping with previous findings (Chown & Nicolson 2004; but see also Bustami, Harrison & Hustert 2002). When the endotracheal PO_2 is above its threshold value and the PCO_2 below its threshold, the spiracles remain closed. If PO_2 declines below and/or PCO_2 rises above their respective thresholds, the spiracles open. Thus, the closed and open phases are easily accounted for. What is new about the model is its demonstration that the flutter phase arises from oscillations around the threshold PO_2 caused by a time delay in the controller feedback. For the species studied (pupae of the Atlas moth, *Attacus atlas*), calculated diffusion time from the spiracle to the segmental ganglion is about 0·5 s, which is in good agreement with empirical data (Förster & Hetz 2010). Thus, hypoxia causes the central sensor to command the spiracles to open, and oxygen enters the system. Owing to the time delay between entry and detection, the oxygen continues entering (and CO_2 leaving) until hypoxia at the sensor is abolished, and the cycle repeats. This F phase continues until the PCO_2 threshold is exceeded and the spiracles open. Apparently random openings often seen in F phase behaviour are likely the consequence of independent control of segmental spiracles by their segmental ganglia and may be less likely if coupling strength (i.e. gas flow along the inter segmental tracheal trunks) among segments is substantial. Thus, an elegant, empirically supported mechanistic model now exists for DGE as an emergent property of two interacting control systems under minimal demand.

Such a model does not account for why, in an adaptive sense, control might revert to the segmental ganglia and show up as DGE in a select group of species. A new 'neural hypothesis' that accounts for the idiosyncracies of the distribution of DGE among the arthropods seems to have resolved this problem. Matthews & White (2011) point out that all of the work thus far on DGE has one thing in common: the individuals being examined have reduced brain activity irrespective of the taxon they are from. This includes anaesthetized or decapitated ants, pupae in diapause and quiescent adults of a range of species. Moreover, according to Matthews & White (2011), the latter typically belong to groups with enlargements of the brain known as mushroom bodies. In turn, brain activity is energetically expensive, with the visual system of flies accounting for as much as 20% of resting metabolic rate (Lehmann & Schützner 2010). Apparently, large brains (i.e. those with mushroom bodies) are especially energetically demanding, although this proposition is speculative. Thus, whenever energetic considerations promote downregulation of metabolic rate, brain activity is reduced, and DGE arises as a consequence of respiratory control being relinquished to the segmental ganglia of the thorax and abdomen. At this point, the interaction between segmental PO_2 sensors and the spiracle-based PCO_2 sensors, so cleverly elucidated by Förster & Hetz (2010), sets in.

The neural hypothesis therefore incorporates both a non-adaptive mechanistic component – interacting control systems – and an adaptive one – energy savings – so reuniting evolutionary and mechanistic explanations within a single testable framework. This framework also provides a means for testing the idea that gas exchange patterns form a continuum – separate reduction in metabolic rate and brain activity by various means, such as low temperature treatments and anaesthesia, might enable the competing mechanisms to be disentangled (Matthews & White 2011). Likewise, the idea that DGE may be especially significant for animals with high spiracular conductance and/or low metabolic rates (Moerbitz & Hetz 2010), which might lead to the risk of oxidative damage, can also be distinguished experimentally from the neural hypothesis using similar approaches on different taxa in a comparative framework.

Broader implications

From an evolutionary perspective, a coupling of the neural hypothesis with the mechanistic basis for interacting controller systems may also explain the presence of DGE in other arthropod groups, such as some scolopendromorph centipedes (Klok, Mercer & Chown 2002), solifuges (Lighton & Fielden 1996) and ticks (Lighton, Fielden & Rechav 1993). In the former case, most other centipedes do not have occludable spiracles, thus preventing the kinds of partial pressure changes, required of the mechanistic interacting set points model, from being established. In the scolopendromorphs, the same energetic considerations and relinquishing of control to the segmental ganglia (Lewis 1981) are likely to be involved. For ticks and solifuges, the neural hypothesis has obvious application: ticks spend much time in an energy conservation state as sit and wait feeders, and solifuges have an energetically highly variable life history and well-developed

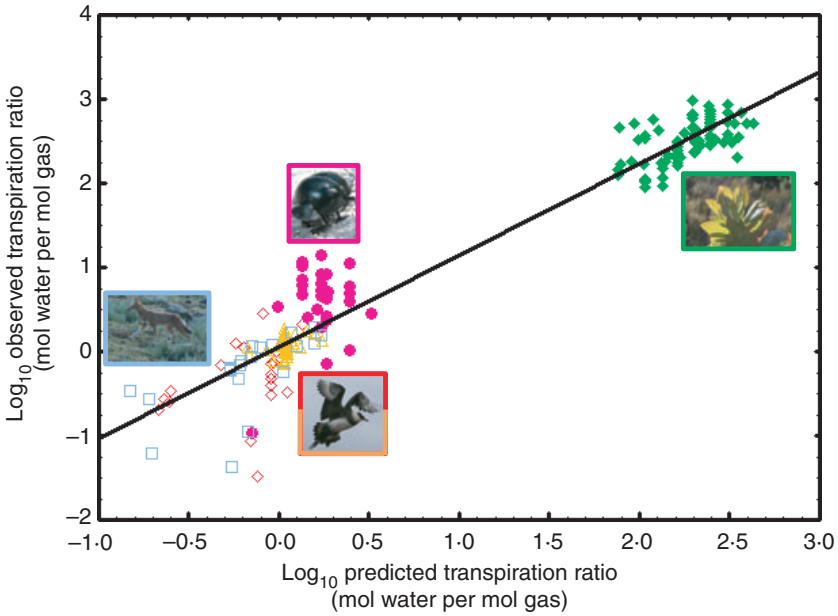


Fig. 2. The observed transpiration ratio (mol water per mol gas) and that predicted by a new, universal model for the water costs of gas exchange (Woods & Smith 2010), for birds and their eggs (open red diamonds and orange triangles, respectively), mammals (blue squares), insects (pink circles) and plants (filled green diamonds). The solid line is a least-squares best fit. Note that the observed values for insects are much higher than those predicted, indicating something of a profligate water strategy. More than half of the data for insects include species with discontinuous gas exchange. Redrawn using the data from the Supplementary Information provided by Woods & Smith (2010).

neural system that might similarly necessitate an energy conservation strategy (Punzo 1998).

With respect to the other evolutionary hypotheses proposed to explain the DGE, two perspectives can be adopted. The first is that DGE seems to necessitate much more of a water loss than is necessary during gas exchange, nicely illustrated by a new, universal model of the water costs of gas exchange (Woods & Smith 2010). For a given metabolic rate, the model typically under predicts water loss in insects, for which most of the data were acquired from studies of insects showing DGE (Fig. 2). An unnecessarily high water loss rate associated with an energy-saving mechanism might therefore mean strong selection for modification of components of the DGE, such as for a prolonged closed phase (Chown & Davis 2003), to reduce as far as possible the water penalty. Therefore, the variation among the DGE components that has long been the subject of investigation and controversy might have arisen because of the water profligate energy-saving mechanism that is DGE, rather than primarily as a water-saving strategy. A similar point was mooted by Lighton (1998) more than a decade ago and might therefore be termed 'Lighton's paradox'. Alternatively, a pre-existing DGC could be pressed into service for many other purposes, such as for water saving or for the limitation of oxidative damage (Chown 2002; Matthews & White 2011), so disentangling origins from maintenance and enabling several factors to act in concert with influence patterns of gas exchange.

From an ecological perspective, the higher than necessary water costs associated with DGE (Woods & Smith 2010) and its common occurrence in the majority of the most species-rich insect orders are troubling. If ectotherm metabolic rates have increased to the extent that seems plausible for current and forecast increases in temperature (Dillon, Wang & Huey 2010), a water penalty may become more of a problem for small ectotherms, such as insects, than an energy one. Indeed, both cuticular and respiratory water loss increase sharply with temperature (Hadley 1994; Chown 2002; Gibbs 2002; Terblanche, Clusella-Trullas & Chown 2010). Elevated desiccation stress may be especially significant where rising temperatures are accompanied by declining rainfall, as seems likely in many regions (Fung, Lopez & New 2011). Whether a switch to cyclic or continuous gas exchange at higher metabolic rates will offset water loss associated with the increase in metabolism is far from clear (Gibbs & Johnson 2004; Lighton & Turner 2008; Williams *et al.* 2010). Likewise, whether acclimatization, which so commonly leads to long-term declines in metabolic rates despite elevated temperatures (Cossins & Bowler 1987), will overcome the increases in metabolic rate (and therefore water loss – see also Terblanche, Clusella-Trullas & Chown 2010) forecast on the basis of short-term rate–temperature relationships is also uncertain. These pressing questions make it evident that the study of variation in gas exchange dynamics is not simply an intriguing area in evolutionary physiology but also one with much broader ecological implications, in many ways the very stuff of macrophysiology (Chown, Gaston & Robinson 2004).

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